The evolution of soil-burrowing cockroaches (Blattaria: Blaberidae) from wood-burrowing ancestors following an invasion of the latter from Asia into Australia

Kiyoto Maekawa[1]† , Nathan Lo[2*], Harley A. Rose[3] and Tadao Matsumoto[1]

[1]*Department of Biology, University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902, Japan*
[2]*National Institute of Agrobiological Sciences, 1-2 Owashi, Tsukuba 305-8634, Japan*
[3]*Department of Crop Sciences, University of Sydney, Sydney, NSW 2006, Australia*

Morphologically similar cockroaches in the subfamilies Panesthiinae and Geoscapheinae (Blattaria: Blaberidae) display contrasting feeding habits, behaviour and biogeographical distributions. Panesthiinae, found throughout Asia and Australia, all live in and feed on decaying wood that they burrow into. Geoscapheinae are restricted to Australia and construct and live in burrows in the soil, where they feed on dry leaves taken from the surface. A lack of knowledge about phylogenetic relationships among these cockroaches hinders an understanding of the factors that have shaped the evolution of their diverse lifestyles and biogeography. To address this issue, we sequenced three genes from representatives of nine of the 10 genera in the two subfamilies, and performed phylogenetic analyses. The well-supported topology revealed the Panesthiinae to be paraphyletic with respect to the Geoscapheinae. Soil-burrowing cockroaches appear to have evolved from a lineage of wood burrowers that invaded Australia from the north some time after the merging of the Asian and Australian tectonic plates *ca.* 20 Myr ago. The main factor promoting the evolution of soil burrowing is likely to have been one of the periods of strong aridity that Australia has experienced since the Miocene period.

Keywords: Blaberidae; biogeography; phylogeny; Wallace's line; Blattaria; cockroaches

1. INTRODUCTION

The cockroach family Blaberidae, originally recognized by McKittrick (1964), contains 11 described subfamilies (Grandcolas 1997). Panesthiinae and Geoscapheinae (Rugg & Rose 1984) are two morphologically similar blaberid subfamilies (figure 1), characterized by their specialized habits of burrowing into wood and soil, respectively (Roth 1982). Panesthiinae comprise six genera that are found only in Asian and Australian regions (figure 1). Like the distantly related cockroach genus *Cryptocercus*, all Panesthiinae members display the uncommon trait among animals of feeding exclusively upon wood that they burrow into. Geoscapheinae comprise four genera, and are found only in Australia (figure 1). All members of this subfamily feed on dry leaf litter, which they transport to permanent burrows constructed up to 90 cm below the surface of the soil. The subfamily's most well-known representative is probably the giant burrowing roach *Macropanesthia rhinoceros* which, at over 30 g, is the heaviest known cockroach on Earth (Matsumoto 1992; Rugg & Rose 1991). Shallow burrowing into sand or soil is known in other cockroaches, though it generally occurs in response to predation or the need for short-term shelter. The burrowing behaviour of Panesthiinae and Geoscapheinae is notable in that it results in the creation of long-term shelters.

Although the two subfamilies display differing overall gross morphologies (figure 1) and behaviour, their taxonomic division is based on only one minor morphological character—the angle of the seventh tergite. Although some studies using molecular techniques have recently been performed on genera within one subfamily (Humphrey *et al.* 1998; Maekawa *et al.* 1999, 2001), no formal examination of relationships between genera from both subfamilies based on modern methods has yet been done. The lack of certainty about their relationships hinders the understanding of how their unique burrowing and feeding habits evolved, as well as the factors that have shaped their current distribution patterns (figure 1). Their strictly Asian and Australian distribution, combined with the fact that they are relatively slow-moving (their legs are adapted for burrowing rather than running), make them good candidates for testing palaeogeographical scenarios associated with Wallace's line. One explanation for their distribution is that the stem group of Geoscapheinae + Panesthiinae evolved in Asia, with the ancestors of Geoscapheinae invading New Guinea/Australia after the collision of the Australian plate with the Asian plate *ca.* 20 Myr ago (Hall 1998). A second possibility is that the stem group evolved in Australia and then a subgroup invaded Asia following the aforementioned collision. A third possibility is that the stem group evolved before the break up of Gondwanaland, perhaps in the region of proximity between India and Australia that existed during that time.

*Author for correspondence (nathanlo@utenti.unimi.it).
† Present address: Dipartimento di Patologia Animale, Igene e Sanità Pubblica Veterinaria, Università di Milano, Via Celoria 10, 20133 Milano, Italy.
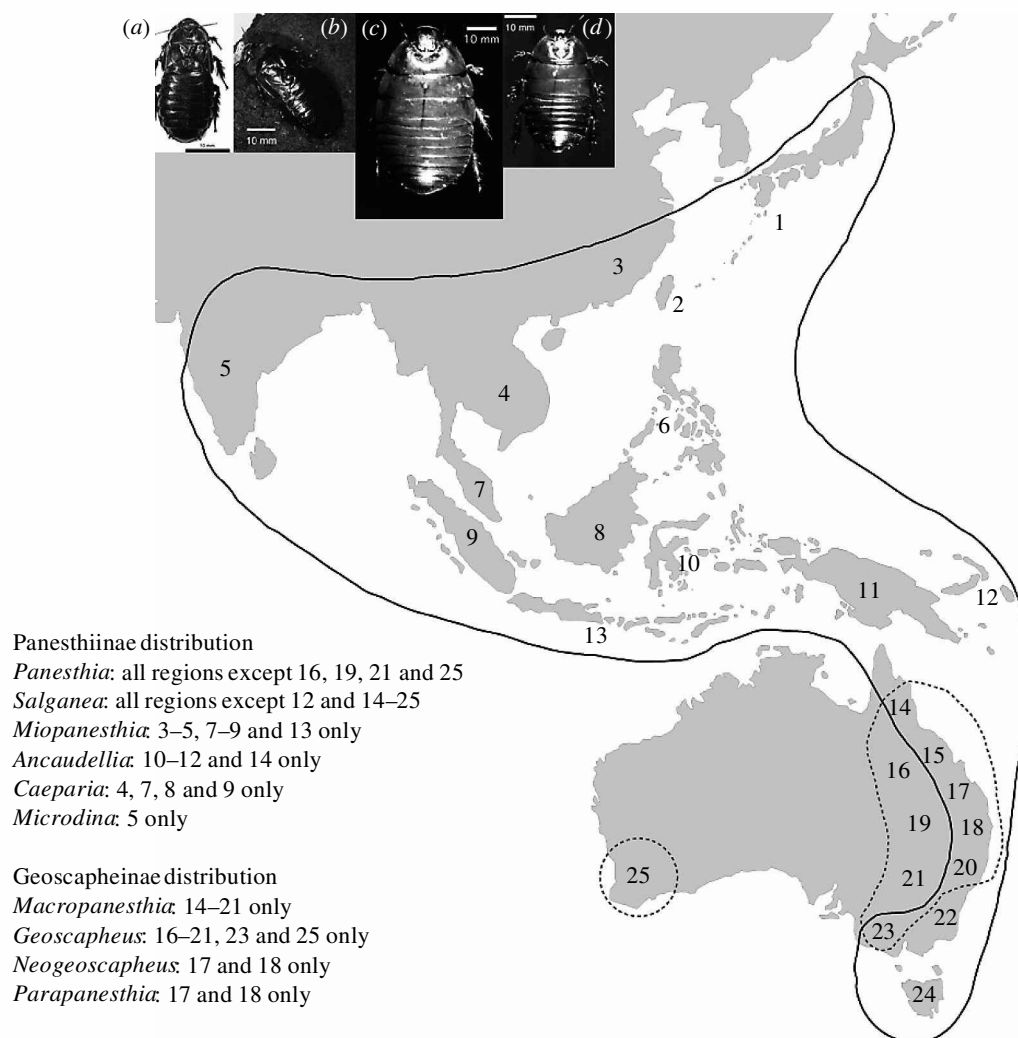
Figure 1. Geographical distribution of Panesthiinae (solid outline) and Geoscapheinae (dotted outlines). Numbers represent the following regions: (1) Japan and the Ryukyu archipelago; (2) Taiwan; (3) east China; (4) Vietnam, Laos, Thailand, Burma and Cambodia; (5) India, Nepal and Bangladesh; (6) Philippines; (7) Malay Peninsula; (8) Borneo; (9) Sumatra; (10) Sulawesi, Molucca Islands; (11) Irian Jaya; (12) Solomon Islands; (13) Java, Lesser Sunda Islands; (14) far north Queensland (QLD); (15) Townsville region; (16) central QLD; (17) Mackay/Rockhampton region; (18) southeast QLD/New South Wales (NSW) border; (19) south inland QLD/northern inland NSW; (20) northern NSW; (21) western NSW/Victoria (22) southern NSW/eastern Victoria; (23) central/western Victoria (24) Tasmania; (25) southern Western Australia. Geoscapheinae are endemic to Australia. *Panesthia lata* is also known from Lord Howe Island, near the east coast of NSW. Distribution shown is according to Roth (1982). Examples of Panesthiinae [Pan] and Geoscapheinae [Geo] are given as follows: (*a*) *Salganea taiwanensis* [Pan]; (*b*) *Panesthia cribrata* [Pan] (photo courtesy of David Rentz); (*c*) *Macropanesthia rhinoceros* [Geo]; (*d*) *Parapanesthia pearsoni* [Geo].

To address the above issues, we have performed the first molecular-phylogenetic examination of Panesthiinae and Geoscapheinae, based on partial sequences of mitochondrial and nuclear genes in 21 taxa representing 9 of their 10 genera. An attempt was also made to examine the phylogenetic position of these subfamilies within the family Blaberidae by using mitochondrial gene sequences.

2. MATERIAL AND METHODS

(a) *DNA extraction, PCR and sequencing*

The species examined in this study, their places of collection, PCR primers for gene amplification and GenBank accession numbers for each of the genes sequenced are given in electronic Appendix A (available on The Royal Society's Publications Web site). Total genomic DNA extraction, PCR conditions, purifi-

cation and sequencing were exactly as described previously (Maekawa *et al.* 1999).

(b) *Establishing the phylogenetic placement of Panesthiinae and Geoscapheinae among other blaberid cockroaches*

Portions of mitochondrial 16S rDNA (hereafter termed 16S) and 12S rDNA (12S) in five Panesthiinae and Geoscapheinae taxa as well as a Perisphaerinae representative were sequenced and aligned with homologous regions in representatives of seven of the other eight currently recognized blaberid subfamilies (Kambhampati 1995). The only subfamily not included in the study was Gyninae (Grandcolas 1997). Alignment of sequence datasets was performed taking into consideration the proposed secondary structures of *Drosophila yakuba* 12S (Neefs *et al.* 1991) and *D. melanogaster* 16S (De Rijk *et al.* 1999),

respectively. Regions that could not be aligned unambiguously were discarded from phylogenetic analyses (see below). A total of 21 blaberid taxa were included in the phylogenetic analyses. Sequences from representatives of the Blattellidae—a separate cockroach family, believed to be closely related to or paraphyletic with respect to Blaberidae (McKittrick 1964; Kambhampati 1995; Klass 1995, 1997, 2001; Grandcolas 1996)—were included in analyses as outgroups and to test the monophyly of Blaberidae.

(c) *Relationships among Panesthiinae and Geoscapheinae*

Partial regions of 12S and nuclear 18S rDNA (hereafter termed 18S), as well as the full mitochondrial cytochrome oxidase II (COII) gene, were amplified and sequenced in 21 members of Geoscapheinae and Panesthiinae. For phylogenetic analyses of each of the three genes, the putative homologous sequences from *Schultesia lampyridiformis* and *Trichoblatta pygmaea* were used as outgroups (not constrained to be monophyletic). These were chosen based on the results of blaberid phylogenetic analysis (see below), which clearly showed that they were phylogenetically distinct from Panesthiinae and Geoscapheinae representatives. 12S sequences were aligned based on the blaberid 12S alignment described above. COII and 18S were aligned by using CLUSTAL X (Thompson *et al.* 1997) and adjusted manually, the latter with the aid of a previously reported dictyopteran sequence alignment (Lo *et al.* 2000).

(d) *Phylogenetic analyses*

Phylogenetic analyses were performed under Bayesian, maximum-parsimony (MP) and maximum-likelihood (ML) criteria. To verify that each dataset contained significantly more hierarchic structure than random data, we measured the skew (g_1) in the distributions of tree lengths for each gene, based on 1000 random generated trees ('generate trees option' in PAUP* 4.0b8; Swofford 2000). The significance of g_1-values was assessed by using the critical values for four-state character data listed previously (Hillis & Huelsenbeck 1992). To check for potential variations in base composition among the sequences in each dataset, the χ^2-test for stationarity in TREEPUZZLE 5.0 was used (Strimmer & Haeseler 1996). Tree topologies were estimated under Bayesian criteria by using the program MRBAYES 2.1 (Huelsenbeck & Ronquist 2001). Parameters for the selected model of substitution (MODELTEST 3.06; Posada & Crandall (1998)) were estimated from the data. A total of 6000 trees was obtained (ngen = 60 000, samplefreq = 10), and, depending on the dataset, the first 1000–3000 of these were considered as the 'burn in' and discarded. A 50% majority-rule consensus tree of the remaining trees was produced. Branch lengths for this consensus tree were calculated in PAUP* under ML criteria, estimating parameters from the data. MP trees were estimated heuristically in PAUP* by using default options with five random addition replicates. Fifty per cent majority-rule bootstrap trees were also produced (1000 replicates, 10 random addition replicates per bootstrap replicate) to provide additional measures of branch reliability. All characters were weighted equally, and gaps were treated as a fifth base. Before the combination of data from different genes for analysis, MP bootstrap trees for individual genes were checked for the presence of conflicting clades with greater than 50% support. This method was chosen because of the uncertainties about other MP and ML congruence tests currently available (Clark *et al.* 2000; Dolphin *et al.* 2000; Yoder *et al.* 2001).

To test alternative phylogenetic hypotheses, the Templeton test (MP) and Shimodaira–Hasegawa test (ML) were used, with the parsimony or likelihood scores of competing topologies compared statistically at the 5% level of significance. Finally, preliminary estimates of divergence times were calculated for some Panesthiinae and Geoscapheinae taxa based on the rate of transversional changes in the COII gene (0.07–0.15% Myr^{-1}) of other insects (Beckenbach *et al.* 1993; Maekawa *et al.* 2001). Clock-like behaviour of the COII gene in the taxa under consideration was tested by using the likelihood-ratio based clock test in TREEPUZZLE 5.0.

3. RESULTS

A comparison of cockroach 12S and 16S mitochondrial rRNAs with their respective putative homologues in *D. yakuba* and *D. melanogaster* revealed that the cockroach sequences contain all the putative structural elements proposed to occur in the fly sequences, with the exception of structural element 39 in the 12S fragments (see electronic Appendix A). Owing to the high level of conservation in the 18S sequences of Panesthiinae and Geoscapheinae members, only a 155 bp region (in which substitutions were present) was examined; this region corresponds to structural elements E23_1 through E23_5 in *D. melanogaster* 18S rRNA (Van de Peer *et al.* 1998). Very few gaps were found among the 18S sequences examined, and alignment was straightforward and unambiguous.

Phylogenetic information for each of the five datasets examined during this study is given in the electronic Appendix. For all datasets, a significant phylogenetic signal was found, with skew values below the critical values for significance at the $p < 0.01$ level (Hillis & Huelsenbeck 1992). All datasets contained sequences that did not significantly differ in base composition, based on the test performed in TREEPUZZLE 5.0. All mitochondrial COII sequences examined contained uninterrupted open reading frames, indicating that they were not nuclear pseudogenes.

(a) *Relationships among Blaberidae subfamilies*

An examination of MP bootstrap trees for each of the two genes 12S and 16S revealed no conflict between clades from each of the topologies, and thus the data were combined. Figure 2 shows the Bayesian 50% majority rule consensus tree obtained from these data, from 10 of the 11 accepted Blaberidae subfamilies. The strict consensus of three equally parsimonious trees was almost identical to that shown, with the exception of relationships among the outgroup taxa. A 99% posterior probability was found for the monophyly of Blaberidae within a paraphyletic Blattellidae, although this clade was not supported by MP bootstrap analysis. Strong support was found for the monophyly of Panesthiinae + Geoscapheinae, with the former being paraphyletic with respect to the latter. Support was found in Bayesian analysis for a sister-group relationship between the examined Zetoborinae + *Phoetalia pallida* (Epilamprinae) and Panesthiinae + Geoscapheinae, but this clade was not supported by bootstrap analysis. The topologies found in Bayesian and MP analyses were in agreement with taxonomic designations in many cases; however, evidence was found for paraphyly of Epilamprinae.
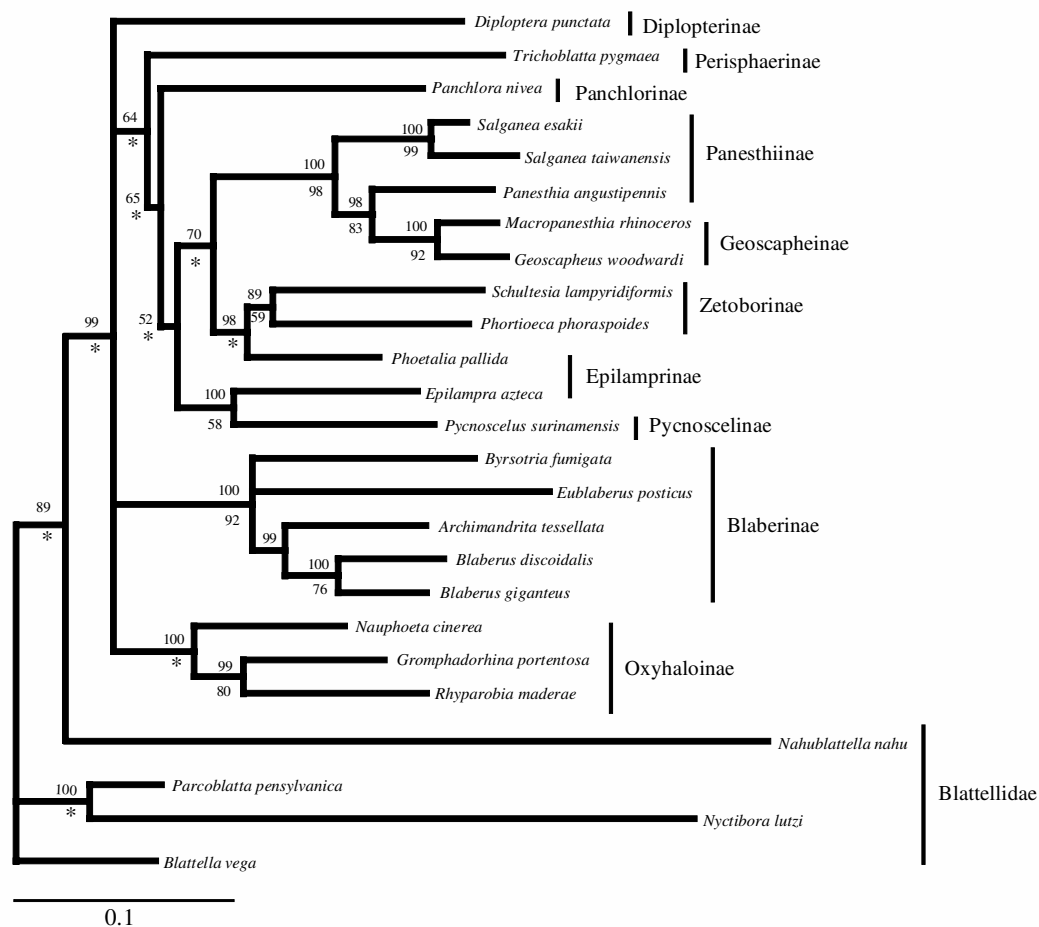
Figure 2. Phylogeny of Blaberidae subfamilies inferred from partial 12S and 16S mitochondrial rDNA sequences. The topology shown was obtained by using Bayesian inference of phylogeny, using the GTR + G model of substitution. Posterior probabilities (PP), expressed as percentages, are shown above branches to indicate the level of support for each node. Branches with less than 50% PP were collapsed to form polytomies. Bootstrap values (expressed as percentages) from a MP analysis are shown below nodes. The asterisks indicate nodes that were not supported in greater than 50% of MP bootstrap replicates. The scale bar indicates the number of inferred substitutions per site. Subfamily designations are indicated adjacent to species names. Representatives of the family Blattellidae were included to test the monophyly of Blaberidae.

(b) *Relationships among Panesthiinae and Blaberidae taxa*

No cases of topological incongruence were found when 50% majority-rule bootstrap trees estimated from each of the three genes 12S, COII and 18S were compared. Figure 3 shows the topology of 21 Panesthiinae and Geoscapheinae members based on the three combined sequences, estimated by using Bayesian analysis. A basal trichotomy between *Miopanesthia*, *Salganea* (each of these two genera being monophyletic) and a clade comprising the remaining genera was found. Within the latter clade, the most basal dichotomy separates some Panesthiinae from a group comprising others as well as the Geoscapheinae. Thus, the Panesthiinae were found to be paraphyletic with respect to the Geoscapheinae. The strict consensus of two equally parsimonious trees was identical to that shown in figure 3, with the exception that there was a basal dichotomy between the *Miopanesthia* clade and all other taxa (supported by 60% of bootstrap replicates). The monophyly of the Geoscapheinae was found in Bayesian analysis and in the shortest MP trees. This clade was not supported in bootstrap analysis; however, downweighting of COII third codon transitions by a factor of 4 relative to other substitutions (Maekawa *et al.* 1999) resulted in

bootstrap support of 70% for it. By using the Templeton (1983) test, the topology in figure 3 (1665 steps) was found to be significantly more parsimonious ($p = 0.0013$) than an alternative *a priori* topology (1692 steps) in which the two subfamilies were each constrained to be monophyletic (apart from this constraint, relationships in figure 3 were held constant). Similarly, a Shimodaira–Hasegawa (1999) test found the paraphyly of the Panesthiinae with respect to the Geoscapheinae to be significant at the 5% level (likelihood scores: 8914.76 and 8945.02; $p = 0.005$).

A preliminary estimate of the divergence time between the clade containing Geoscapheinae and that containing *Ancaudellia* and *Panesthia* spp. (excluding *P. transversa*) was obtained as follows. First, a test for clock-like evolution in the COII gene of these taxa was performed in TREEPUZZLE 5.0 by using the TN+I+G model of substitution, with *P. transversa* as the outgroup. The lnL of the tree without clock was -3248.49, whereas that with clock was -3256.23. Based on a likelihood ratio test, the simple clock-like tree could not be rejected at the 5% level. Second, the transversion distance percentages in the COII gene for one member of each of the two clades (Geoscapheinae and *Panesthia*/*Ancaudellia* spp.) were calculated, and repeated for each combination. The rate of
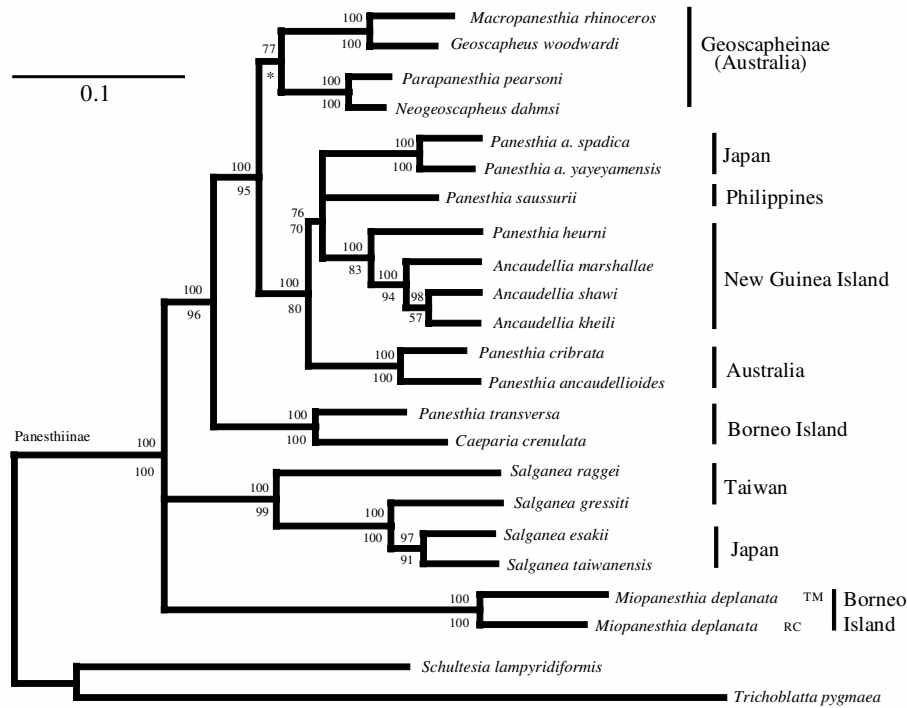
Figure 3. Phylogeny of Panesthiinae and Geoscapheinae inferred from a combined analysis of 12S, COII and 18S, obtained by using Bayesian inference of phylogeny with the GTR+I+G model of substitution. Posterior probabilities (PP), expressed as percentages, are shown above branches to indicate the level of support for each node. Branches with less than 50% PP were collapsed to form polytomies. Bootstrap values (expressed as percentages) from a MP analysis are shown below nodes. The asterisk indicates a node that was not supported in more than 50% of bootstrap replicates; however, an analysis in which COII third codon transitions were downweighted by a factor of 4 resulted in 70% support. The scale bar indicates the number of inferred substitutions per site.

change of this figure in the COII gene of various *Drosophila* spp. has been estimated to range from 0.0007 to 0.0015 changes per site per Myr. The average transversion distance between the Geoscapheinae and *Ancaudellia/Panesthia* clade was found to be 0.038 ± 0.005 changes per site ($n = 36$), which suggests that these clades diverged somewhere between 12.7 and 27.1 Myr ago. Based on similar calculations, the two clades of Geoscapheinae are estimated to have diverged in the same time-frame, although the lower number of taxa is likely to make this estimate less reliable.

4. DISCUSSION

To test the assumed monophyly of Panesthiinae + Geoscapheinae, and to find suitable outgroups for a closer examination of these two subfamilies, we performed a preliminary analysis of relationships among 10 of the 11 subfamilies in Blaberidae (figure 2). Members of Panesthiinae + Geoscapheinae formed a well-supported monophyletic group in Bayesian and MP analyses of both 12S and 16S; however, relationships among other blaberid subfamilies were less well-resolved. The closest group to Panesthiinae + Geoscapheinae was Zetoborinae + *P. pallida*, which is interesting given that Zetoborinae are known to contain a few wood-burrowing species (e.g. Pellens *et al.* 2002). The possibility thus exists that the last common ancestor of these four groups had this characteristic. Further systematic studies involving more genes and taxa from Zetoborinae and Epilamprinae, combined with comparisons of the life habits of these cockroaches (Grandcolas 1998) should shed further light on this issue.

More detailed analysis of Panesthiinae and Geoscapheinae based on three genes (figure 3) provided a well-corroborated estimate of relationships in these subfamilies. Compelling evidence in the form of bootstrap support, posterior probabilities and statistical tests was found for Panesthiinae being paraphyletic with respect to Geoscapheinae, a result that is not obvious based on overall morphology and behavioural characteristics. All *Miopanesthia* and *Salganea* species, as well as *P. transversa* + *C. crenulata* are found only in Asia and feed on decaying wood. The phylogenetic position of these taxa in figure 3 indicates that the ancestors of Panesthiinae had similar characteristics. Two more subordinate clades were found as sister group to *P. transversa* + *C. crenulata*: one containing *Ancaudellia* and *Panesthia* taxa, and the other containing Australian endemic Geoscapheinae. Owing to the primarily Asian distribution of most Panesthiinae and the subordinate position of the strictly Australian Geoscapheine, we suggest that the ancestors of the latter invaded Australia from the north. A recent phylogenetic study of elapid snakes from regions including Asia and Australia also found evidence for the migration of taxa from the former region into the latter (Keogh *et al.* 1998). Such migrations would have been possible at various times in the past 20 Myr, after the Australian plate collided with the Asian plate in the region of present day Sulawesi (Hall 1998). Preliminary estimates of the divergence time (12.7–27.1 Myr ago) between the lineages leading to *Panesthia/Ancaudellia* spp. (excluding *P. transversa*) and Geoscaphainae did not allow us to determine whether the split occurred before or after the aforementioned collision. We are aware of the potential problems with using rates

of sequence change from distantly related taxa to infer divergence dates, and we are now performing further studies using the intracellular *Blattabacterium* spp. of cockroaches to obtain more reliable estimates of divergence dates (Moran *et al.* 1993).

The ancestors of Geoscapheinae that invaded Australia would have been wood-feeders, most likely living on decaying wood in the tropical and temperate forests of northern Australia. The topology of figure 3 indicates that, at some point in the past, the ancestors of the Geoscapheinae began the shift in behaviour from living in and feeding on wood, to digging burrows in the soil and feeding on dry leaf litter. What environmental factors might have caused such adaptations? Clues can be obtained by considering the history of the region Geoscapheinae are found in, which is primarily the northeastern region of Australia. It is believed that from the middle Miocene until the Pliocene, (15–5 Myr ago), an expansion of the Antarctic ice sheet caused colder conditions and a drop in rainfall across the Australian continent, which led to increasing levels of aridity (Frakes *et al.* 1987). During the Miocene, the aridity spread from the south as a belt of anticyclonic circulation developed at high latitudes and migrated north (Adam 1992). At the beginning of the Pliocene, a brief period of warm and moist conditions occurred, which was followed by strong periods of aridity. It is likely that the ancestors of Geoscaphinae were exposed to arid conditions during at least one of the aforementioned periods. Such aridity caused a drop in the amount of temperate and rainforest cover and led to the dominance in many areas of grassland and xeric vegetation (Heatwole 1987). The consequent reduction in the normal habitat of Panesthiinae would have provided selection pressure for the adoption of new feeding strategies. Dry surface conditions would have favoured the movement of Geoscapheinae ancestors underground, where humid conditions could be obtained. Having legs adapted to burrowing into wood would have facilitated their burrowing into soil. Presumably, as the number of rotting logs decreased due to aridity, the xeric vegetation that had replaced them provided dry leaf litter on which the evolving soil burrowers could feed.

Interestingly, the Geoscapheinae are not the closest relatives of the Australian wood-feeding *Panesthia* spp. Instead, the latter are more closely related to *Panesthia* and *Ancaudellia* spp. from various parts of Asia, ranging from Japan to New Guinea. This suggests that they invaded Australia independently of the ancestors of Geoscapheinae. Alternatively, the entire group containing Geoscapheinae + *Ancaudellia* + *Panesthia* (excluding *P. transversa*) might have evolved in Australia after an invasion of their last common ancestor from the north, with the reverse migration of *Panesthia* and *Ancaudellia* spp. to the north. More detailed studies on *Panesthia* and *Ancaudellia* taxa should shed light on this issue. In either case, it might be expected that other wood-feeding cockroaches from Australia or perhaps New Guinea will be identified as the closest relatives of Geoscapheinae. We are currently expanding our study of taxa in these areas to address this issue. In light of the consistent molecular support for the Panesthiinae being paraphyletic with respect to the Geoscapheinae, we suggest that the subfamily status of the latter be abandoned, with the four genera being placed in the subfamily Panesthiinae.

REFERENCES

Adam, P. 1992 *Australian rainforests*. New York: Oxford University Press.

Beckenbach, A. T., Wei, Y. W. & Liu, H. 1993 Relationships in the *Drosophila obscura* species group, inferred from mitochondrial cytochrome oxidase II sequences. *Mol. Biol. Evol.* **10**, 619–634.

Clark, M. A., Moran, N. A., Baumann, P. & Wernegreen, J. J. 2000 Cospeciation between bacterial endosymbionts (*Buchnera*) and a recent radiation of aphids (*Uroleucon*) and pitfalls of testing for phylogenetic congruence. *Evolution* **54**, 517–525.

De Rijk, P., Robbrecht, E., de Hoog, S., Caers, A., Van de Peer, Y. & De Wachter, R. 1999 Database on the structure of large subunit ribosomal RNA. *Nucleic Acids Res.* **27**, 174–178.

Dolphin, K., Belshaw, R., Orme, C. D. L. & Quicke, D. L. J. 2000 Noise and incongruence: interpreting results of the incongruence length difference test. *Mol. Phylogenet. Evol.* **17**, 401–406.

Frakes, L. A., McGowran, B. & Bowler, J. M. 1987 Evolution of Australian environments. In *Fauna of Australia* (ed. G. R. Dyne & D. W. Walton), pp. 1–16. Canberra: CSIRO.

Grandcolas, P. 1996 The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Can. J. Zool.* **74**, 508–527.

Grandcolas, P. 1997 The monophyly of the subfamily Perisphaerinae (Dictyoptera: Blattaria: Blaberidae). *Syst. Entomol.* **22**, 123–130.

Grandcolas, P. 1998 The evolutionary interplay of social behaviour, resource use and anti-predator behaviour in Zetoborinae + Blaberinae + Gyninae + Diplopterinae cockroaches: a phylogenetic analysis. *Cladistics* **14**, 117–127.

Hall, R. 1998 The plate tectonics of Cenozoic South East Asia and the distribution of land and sea. In *Biogeography and geological evolution of south east Asia* (ed. R. Hall & J. D. Holloway), pp. 99–131. Leiden: Backbuys Publishers.

Heatwole, H. 1987 Major components and distributions of the terrestrial fauna. In *Fauna of Australia* (ed. G. R. Dyne & D. W. Walton), pp. 101–115. Canberra: CSIRO.

Hillis, D. M. & Huelsenbeck, J. P. 1992 Signal, noise, and reliability in molecular phylogenetic analyses. *J. Hered.* **83**, 189–195.

Huelsenbeck, J. P. & Ronquist, F. 2001 MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**, 754–755.

Humphrey, M., Colgan, D. J. & Rose, H. A. 1998 Electrophoretic studies of cockroaches of the Australian endemic subfamily Geoscapheinae. *Zool. J. Linn. Soc.* **124**, 209–234.

Kambhampati, S. 1995 A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. *Proc. Natl Acad. Sci. USA* **92**, 2017–2020.

Keogh, J. S., Shine, R. & Donnellan, S. 1998 Phylogenetic relationships of terrestrial Australo-Papaun elapid snakes (Subfamily Hydrophiinae) based on cytochrome *b* and 16S rRNA sequences. *Mol. Phylogenet. Evol.* **10**, 67–81.

Klass, K. D. 1995 Die Phylogeny der Dictyoptera. PhD thesis, Ludwig Maximilians Universität, Cuvillier, Göttingen.

Klass, K. D. 1997 The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonn. Zool. Monogr.* **42**, 1–341.

Klass, K. D. 2001 Morphological evidence on blattarian phylogeny: 'phylogenetic histories and stories' (Insect, Dictyoptera). *Dt. Ent. Z.* **48**, 223–265.

Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C. & Noda, H. 2000 Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Curr. Biol.* **10**, 801–804.

McKittrick, F. A. 1964 Evolutionary studies of cockroaches. *Mem. Cornell Univ. Agr. Exp. Stn* **389**, 1–197.

Maekawa, K., Lo, N., Kitade, O., Miura, T. & Matsumoto, T. 1999 Molecular phylogeny and geographic distribution of wood-feeding cockroaches in east Asian islands. *Mol. Phylogenet. Evol.* **13**, 360–376.

Maekawa, K., Kon, M., Araya, K. & Matsumoto, T. 2001 Phylogeny and biogeography of wood-feeding cockroaches, genus *Salganea* Stål (Blaberidae: Panesthiinae), in southeast Asia based on mitochondrial DNA sequences. *J. Mol. Evol.* **53**, 651–659.

Matsumoto, T. 1992 Familial association, nymphal development and population density in the Australian giant burrowing cockroach, *Macropanesthia rhinoceros* (Blattaria: Blaberidae). *Zool. Sci.* **9**, 835–842.

Moran, N. A., Munson, M. A., Baumann, P. & Ishikawa, H. 1993 A molecular clock in endosymbiotic bacteria is calibrated using the insect hosts. *Proc. R. Soc. Lond.* B **253**, 167–171.

Neefs, J. M., Van De Peer, Y., de Rijk, P., Goris, A. & De Wachter, R. 1991 Compilation of small ribosomal subunit RNA sequences. *Nucleic Acids Res.* **19**(Suppl.), 1987–2015.

Pellens, R., Grandcolas, P. & Domingos da Silva-Neto, I. 2002 A new and independently evolved case of xylophagy and the presence of intestinal flagellates in the cockroach *Parasphaeria boleriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of the Brazilian Atlantic forest. *Can. J. Zool.* **80**, 350–359.

Posada, D. & Crandall, K. A. 1998 MODELTEST: testing the model of DNA substitution. *Bioinformatics* **14**, 817–818.

Roth, L. M. 1982 A taxonomic revision of the Panesthiinae of the world. IV. The genus *Ancuadellia* Shaw, with additions to parts I–III, and a general discussion of distribution and relationships of the components of the subfamily (Dictyoptera: Blattaria, Blaberidae). *Aust. J. Zool.* **82**(Suppl. Ser. 82), 1–142.

Rugg, D. & Rose, H. A. 1984 The taxonomic significance of reproductive behaviour in some Australian cockroaches (Blattodae: Blaberidae). *J. Aust. Entomol. Soc.* **23**, 118.

Rugg, D. & Rose, H. A. 1991 Biology of *Macropanesthia rhinoceros* Saussure (Dictyoptera: Blaberidae). *Ann. Entomol. Soc. Am.* **84**, 575–582.

Shimodaira, H. & Hasegawa, M. 1999 Multiple comparisons of log-likelihoods with applications to phylogenetic inferences. *Mol. Biol. Evol.* **16**, 1114–1116.

Strimmer, K. & von Haeseler, A. 1996 Quartet puzzling: a quartet maximum likelihood method for reconstructing tree topologies. *Mol. Biol. Evol* **13**, 964–969.

Swofford, D. L. 2000 PAUP*: *phylogenetic analysis using parsimony (*and other methods)*. Sunderland, MA: Sinauer Associates.

Templeton, A. R. 1983 Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. *Evolution* **37**, 221–244.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G. 1997 The CLUSTAL:X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res.* **25**, 4876–4882.

Van de Peer, Y., Caers, A., De Rijk, P. & De Wachter, R. 1998 Database on the structure of small ribosomal subunit RNA. *Nucleic Acids Res.* **26**, 179–182.

Yoder, A. D., Irwin, J. A. & Payseur, B. A. 2001 Failure of ILD to determine data combinability for slow loris phylogeny. *Syst. Biol.* **50**, 408–424.